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STUDIES IN SCHEFFLERA (ARALIACEAE): THE CEPHALOSCHEFFLERA COMPLEX D. G. FRODIN

IN RECENT YEARS there has been a renewal of interest in the mor-

phology, anatomy, and systematics of the Araliaceae, beginning with the work of Baumann (1946) and continuing to the present (Baumann-Bodenheim, 1955; Rodríguez, 1957; Hoo & Tseng, 1965; Hutchinson, 1967; Smith & Stone, 1968; Eyde & Tseng, 1969, 1971; Grushvitzky & Skvortsova, 1970; Hladik, 1970; Philipson, 1970; Grushvitzky et al., 1971; Tseng, 1973; Bamps, 1974b). This paper, a preliminary report on the complex of sect. CEPHALOSCHEFFLERA Harms and some related topics, represents the first of a series aimed at elucidating the systematics of Schefflera J. R. & G. Forst., the largest and geographically most widespread genus in the family, and one which is conspicuous in many tropical vegetation formations. Although there are several recent regional revisions (Backer & Bakhuizen, 1965; Bamps, 1974a, 1974b; Bernardi, 1969; Grushvitzky & Skvortsova, 1969; Hoo & Tseng, 1965; Li, 1942; Macbride, 1959; Smith, 1944; Smith & Stone, 1968; Tennant, 1968), the latest general revision on a world-wide basis is an incomplete and uncritical compilation by Viguier (1909). In addition, the limits of Schefflera, like those of various other genera in the Araliaceae, have been subject to many differences of opinion, which a perusal of even some of the above-cited references will show.

THE CEPHALOSCHEFFLERA COMPLEX

The first part of this paper is primarily a reconsideration of sect. CEPHALOSCHEFFLERA Harms (1894), which, for convenience, I shall here call "the *Cephaloschefflera* complex." It is a partial summary of an as yet unpublished dissertation (Frodin, 1970), which is in turn based on research toward a world-wide revision of *Schefflera* and allied genera. Associated with this question is the status of *Brassaia* Endl., included by Harms within his sect. CEPHALOSCHEFFLERA but still kept separate from *Schefflera* by a number of authors, both botanical (Burbidge, 1963; Parham, 1964; Hutchinson, 1967; Smith & Stone, 1968; Stone, 1970; Clifford & Ludlow, 1972) and horticultural (Neal, 1965). This may be in part due to tradition (*Brassaia* was recognized as distinct by Bentham (1867)) or convenience. It may be noted that the type species of *Brassaia*, *B. actinophylla* Endl. (= *S. actinophylla* (Endl.) Harms), has long been a well known staple of ornamental horticulture, both indoors and out, and in some countries or regions it is adventive or naturalized (e.g., Fiji,

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Singapore, southern Queensland). The question as to whether Brassaia should be kept separate or should be merged with Schefflera in a way highlights the whole problem of the Cephaloschefflera complex: is it or is it not a natural grouping?

Schefflera is presently considered to have ca. 200 species (Willis, 1973). These species are found in most of the tropical and subtropical regions of the earth, but they are especially numerous in certain mountainous belts, such as the Andes and the mountains of Southeast Asia and Malesia (notably the central cordillera of New Guinea); the other main concentrations are found in the Guayana Highlands, Madagascar, and New Caledonia. The genus is typified by the single species in New Zealand, Schefflera digitata J. R. & G. Forst. As delimited by Harms (1894-97), Schefflera comprises trees, shrubs, epiphytes, hemi-epiphytes (sometimes strangling), and climbers. The genus is largely characterized by the following: a) an absence of prickles on vegetative parts; b) once palmately compound leaves with fused stipules extending into an appendage of greater or lesser length at the base of the petiole; and c) inflorescences in panicles with a main axis and a varying number of branches along which the flowers are arranged in more or less numerous, usually stalked umbellules, capitula, racemules or spicules. Less commonly, the entire inflorescence forms a compound umbel recalling those present in the vast majority of the Umbelliferae. The flowers lack an articulation at the base of the pedicel and are most often characterized by an ovary with five (or more) locules.

Associated with Schefflera are a number of related genera: Crepinella E. March., Didymopanax Decne. & Planchon, Dizygotheca N. E. Br., Enochoria Baker f., Geopanax Hemsley, Neocussonia (Harms) Hutchinson, Octotheca R. Vig., Plerandra A. Gray, Scheffleropsis Ridley, and Tupidanthus Hook. f. & Thomson. Agalma Miq. and Brassaia Endl. are maintained as segregates of Schefflera by Hutchinson (1967), while several authors, past and present, have merely segregated Brassaia. In the Philippines, Merrill (1923) added a further segregate, Cephaloschefflera (Harms) Merr. (based on sect. CEPHALOSCHEFFLERA Harms). All of these taxa are distinguished from one another by essentially small differences in inflorescence morphology and in the absolute and relative numbers of floral parts. More distantly related are Brassaiopsis Decne. & Planchon, Macropanax Miq., and Pseudopanax C. Koch. Harms (1894) proposed the division of Schefflera (as delimited by him) into two sections:

Sect. CEPHALOSCHEFFLERA. Flowers sessile, in more or less densely aggregated capitula, these mostly pedunculate and arranged in racemes [including Brassaia]. (PLATE III-A.) Sect. EUSCHEFFLERA. Flowers pedicellate, in racemes or umbels. (PLATE III-B.)

The geographical distribution of both sections was shown to be more or less pantropical, although sect. CEPHALOSCHEFFLERA was not re-

corded for the islands east of New Guinea. Harms intended his delimitation of sections and subsections to be practical; to him, attempting a natural arrangement at that time was not advisable, since available herbarium material and field data were too often imperfect. Unfortunately, he never made a new overall revision of *Schefflera* before his death in 1942, although in the intervening 48 years he described numerous new species and made various regional revisions, of which the most important was that forming part of his treatment of the Papuasian Araliaceae (Harms, 1920-21).

Harms's arrangement came into wide use, its outlines (although sometimes modified) being used for treatments of *Schefflera* and other Araliaceae in many floras and regional revisions. Initial acceptance of his arrangement may have been consolidated by the wide influence of Engler and Prantl's *Die natürlichen Pflanzenfamilien* and other German works of the pre-World War I era. Since then, the most significant modification of Harms's system has been that of Hoo and Tseng (1965), in which that part of the *Agalma* group characterized by entirely racemose inflorescences was elevated to sectional rank, along with their sect. BRASSAIA (= sect. CEPHALOSCHEFFLERA Harms) and sect. SCHEFFLERA (= sect. EUSCHEFFLERA of Harms, except for the racemosely flowered species in the *Agalma* group); this arrangement has also been adopted by Grushvitzky and Skvortsova (1969).

An alternative arrangement of *Schefflera* was proposed by Viguier (1909). In his compilation he showed that a few species were intermediate in so far as pedicel development was concerned. In other words, the flowers *appeared* to be in capitula, although in fact they were pedicellate. This interpretation cut across the primary division in Harms's scheme, thus rendering it open to question. For the sake of comparison, Viguier's scheme is given below in synoptic form (no formal nomenclature was applied to his groups):

- 1. Styles distinctly developed, united into a column on a more or less convex disk; flowers in racemes or in racemosely arranged umbellules (rarely capitula). [Only one capituliferous species, *Schefflera schumanniana* Harms from New Guinea, was included here; the other members are the *Agalma* group of species of sect. EUSCHEFFLERA Harms.] (PLATES I-A, I-B.)
- Styles none and stigmata sessile on the disk, or styles free or united only at the base, radiating outward in fruit; flowers in racemosely arranged umbellules or capitula.
 - a. Flowers in capitula. [Most members of sect. CEPHALOSCHEFFLERA Harms, including *Brassaia*, were listed here.] (PLATE III-A.)
 b. Flowers in umbellules. [This group included the greater part of sect. EUSCHEFFLERA, except for the *Agalma* group of species.] (PLATES II-A, III-B.)
- Styles variously developed; flowers umbellulate, arranged in compound umbels. [This group included miscellaneous members of sect. EUSCHEFFLERA, mostly from northern South America, Madagascar, and New Caledonia.] (PLATE II-B.)

Viguier regarded the form of the inflorescence and the nature and degree of fusion of the styles as more important attributes than the presence or absence of capitula, a characteristic which was, so to speak, relegated to third place. Apparently, whether or not a given species was considered capituliferous depended, in his view, on the overall *appearance* of the cluster of radiating flowers; whereas Harms maintained a more exact outlook, basing his delimitation on the presence or absence of pedicels. (At a later date, however, Harms appears to have made the delimitation in Viguier's sense; see his treatment of Papuasian *Schefflera* (1920–21, p. 385).)

As already noted, the Philippine species of the *Cephaloschefflera* complex were the first to be elevated to generic rank (Merrill, 1923). However, Hutchinson (1967) proposed that *all* of the capituliferous species be raised to that rank, reinstating *Brassaia* to incorporate them. His distinction was based merely on the presence of capitula as opposed to umbellules, without qualification. In an appendix (1967, pp. 622–624), he listed 45 species as belonging to his expanded concept of *Brassaia*; even then, a great many more published species which should logically have been accounted for were left out. In a similar manner, Hutchinson reinstated Miquel's old genus *Agalma* to include those species of *Schefflera* with flowers racemosely arranged throughout, notwithstanding their other relationships.

Hutchinson's proposals provided the lead which stimulated my studies in the direction of the Cephaloschefflera complex. During field work in New Guinea and New Britain in 1965-66, there first arose the suspicion that the complex as it stood might be an artificial grouping; the relationships of the various species of Schefflera observed, and the groups into which they seemed to fall, appeared not to correspond to the divisions proposed in the literature for the Papuasian species (Harms, 1920-21, 1938; Philipson, 1951). A satisfactory explanation appeared to be that series of capituliferous species were, as groups, more closely related to otherwise similar series of umbelluliferous species in the Papuasian region than they were to other series of capituliferous species in that region or elsewhere. Subsequent research in herbarium and library, covering all 123 described species that should logically be assigned to the Cephaloschefflera complex because of their inflorescence type, has shown that this preliminary hypothesis is correct when applied on a world-wide basis. There are examples of close relationships between umbelluliferous and capituliferous species in the Neotropics, the African region, and mainland Asia, as well as throughout Malesia. In fact, the similarity in the patterns of evolutionary radiation, both in Papuasia and the Andes, each involving umbelluliferous and capituliferous species, is especially striking and merits closer study. A detailed discussion of all observed progressions is beyond the scope of this paper and the cases enumerated below are merely representative.

In the Neotropics, the umbelluliferous species Schefflera ternata Cuatr. of Colombia is closely related to the capituliferous S. herthae Harms of

Ecuador by virtue of its 3-5-foliolate leaves, slender 2-3-branched inflorescences, capitula/umbellules with few flowers, and conical corollas. An example of a gradual transition is that from *S. sphaerocoma* (Bentham) Harms (an umbelluliferous species with moderately long pedicels growing from Costa Rica to Colombia) through *S. sciadophyllum* (Swartz) Harms (an umbelluliferous species with rather short pedicels growing in Jamaica) to the capituliferous *S. robusta* (A. C. Sm.) A. C. Sm. of Costa Rica. The common features of these three species include large leaves with many leaflets, inflorescences with many radiating branches bearing numerous racemosely arranged few-flowered capitula/umbellules, and

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small flowers with elevated disks and short, partially free styles.

In the African region, the capituliferous Geopanax procumbens Hemsley¹ of the Seychelles is more closely related to the umbelluliferous species S. barteri (Seem.) Harms and S. goetzenii Harms from mainland Africa, all three having similar leaf venation, calyptrate corollas with minute sutures, and a 5-10-locular ovary, than to the capituliferous S. mannii (Hooker f.) Harms, S. stolzii Harms, and S. volkensii Harms, all of which have discrete petals and a 5-locular ovary.

In Asia, the umbelluliferous species Schefflera wallichiana (Wight & Arnott) Harms of South India and S. khasiana (C. B. Cl.) Viguier of eastern India to China are very closely related to the capituliferous S. capitata (Wight & Arnott) Harms by virtue of their nearly identical leaflet form and venation, short stipular ligules, sutured calyptrate corollas, inflorescences with a moderate number of branches, stylar column absent or nearly so, and ovary 5-9(-10)-locular. However, S. capitata differs from S. actinophylla by the presence in the latter of four large bracts per flower (in contrast to three in S. capitata), a 10-12locular ovary, elongated anthers, and much longer stipular ligules. The apparent similarity between the two (noted by earlier workers) is due to convergence and is not necessarily indicative of close relationship, although there is evidence that the group of species associated with S. actinophylla are more closely related to this S. wallichiana/S. capitata group than to any other in the Old World. In New Guinea, the capituliferous species Schefflera schumanniana Harms is more closely related to the umbelluliferous S. hellwigiana Harms (the two species having similar habitats in the understory of damp montane forests, shrubby habits, 5-foliolate leaves with strongly reticulate leaflets, slender, few-branched inflorescences, and long-styled globose fruits) than to large, canopy-dwelling, sun-loving capituliferous species such as S. carrii Harms, S. lasiosphaera Harms, S. stolleana Harms, or S. morobeana Harms. Similarly, the capituliferous S. chaetorrhachis Harms is more closely related to the umbelluliferous S. bougainvilleana Harms, both having small green flowers in 60-100-branched inflorescences, than to the capituliferous S. actinophylla or the capituliferous S. pachystyla

¹This taxon should be transferred to *Schefflera*. Availability of better material has enabled me to find that the characters used by Hemsley (1906) to segregate *Geopanax* do not hold.

Harms, both of which have large red or pink flowers and 5-12-branched inflorescences.

Reference should also be made to those "intermediate" species which were first noted by Viguier as not readily fitting into either the capituliferous or umbelluliferous assemblages. His list included the following Malesian species: S. cephalotes (C. B. Cl.) Harms, S. tomentosa (Bl.) Harms, S. scortechinii (King) Viguier, and S. apiculata (Miq.) Viguier. In addition, he considered the neotropical S. heterotricha (Planchon & Linden ex E. March.) Harms ex Viguier, placed by Harms in his sect. EUSCHEFFLERA, to be capituliferous and grouped it with S. trianae (Planchon & Lindley ex E. March.) Harms and S. euryphylla Harms, mentioning that (translated) "in this case it is impossible to trace the limit between the two sections which he [Harms] proposes." He also noted that "for example, S. cephalotes of Malaya, of his [Harms's] section CEPHALOSCHEFFLERA, has distinctly pedicellate flowers." Since Viguier's time, more "intermediate" species have come to light, among them S. angiensis Gibbs of New Guinea, S. merrillii Elmer of the Philippines, and S. chinensis (Dunn) Li of western China. In addition, it has become evident that the flowers in the immature inflorescences of many species that are umbelluliferous when mature appear to be in capitula, since evident pedicel elongation has not yet taken place. Furthermore, there are a number of examples of both capituliferous and umbelluliferous species in which further pedicel development can take place after anthesis; e.g., S. cephalotes, S. barteri, and S. versteegii Harms of New Guinea. In some species the flowers, although forming capitula, are found to be distinctly pedicellate when the capitula are bisected; this is seen in S. cephalotes, as noted by Viguier, and in S. lasiosphaera of New Guinea. A further list of "intermediate" species has been given by Jacques-Felix (1970). While recognizing that the existence of these "intermediates" cast doubt on the validity of Harms's primary divisions in Schefflera, Viguier did not attempt a more thorough analysis of relationships at the species level. However, the evidence now available has made possible the "linking" of most of the intermediates with other species. Schefflera cephalotes is in leaf, inflorescence, and fruit characters most closely linked with the umbelluliferous S. havilandii Merr. of Borneo and S. latifoliolata (King) Viguier of Malaya; S. tomentosa appears to be close to the umbelluliferous S. yatesii Merr. of Sumatra and Malaya and S. petiolosa (Miq.) Viguier of Borneo in leaflet, inflorescence, and fruit characters; S. apiculata seems quite close to the umbelluliferous Moluccan species of Schefflera now known as Brassaia littorea Seem.; and S. scortechinii is but a phase of the umbelluliferous S. hullettii (King) Viguier of Malaya and Sumatra, with immature inflorescences. These umbelluliferous species do not on any account belong to the same series or even the same section. The affinities of S. heterotricha are more obscure. Related taxa may include Didymopanax allocotanthus Harms of Bolivia and Schefflera rubiginosa (Decne. & Planchon ex Harms) Steyerm. [non

Ridley] of Colombia and Venezuela; all have elongated styles with five (or two) radiating stigmata and a 5-toothed calyx. Schefflera chinensis is closer to the umbelluliferous S. hypoleucoides Harms of northern Viet Nam and S. hypoleuca (Kurz) Harms of eastern India to China than to any other capituliferous species, the three taxa having relatively similar leaf form, inflorescence, and fruit; collectively, however, the three are amply distinct from species such as S. cephalotes, with which Hoo and Tseng (1965) tried to link S. chinensis.

Section CEPHALOSCHEFFLERA (including Brassaia), as proposed by Harms and more or less modified by him and later authors, is thus manifestly an evolutionary grade (Huxley, 1958; Simpson, 1961). The probable direction of evolution has been in the gradual reduction and suppression of pedicels in different series of species, perhaps by successive retardations of pedicel growth during development of the inflorescence before and after anthesis. Whether or not this is associated with changes in pollination and/or dispersal mechanisms and, if so, what kinds of mechanisms are involved, I am unable to determine at present.² It may be noted here that the occurrence of capitula in the Araliaceae (apart from Schefflera) is generally relatively uncommon. Only the neotropical Oreopanax, the Pacific-insular Meryta, and the essentially eastern Malesian/Melanesian Boerlagiodendron and Osmoxylon are wholly or partially made up of species with capituliferous inflorescences. Within Schefflera the only series of capituliferous species without close relatives amongst umbelluliferous species is the Brassaia group (in the strict sense), the type species of which is S. actinophylla. The geographical range of these species is centered in Papuasia. As a group, the species are very distinctive, with fruits black at maturity and brilliantly-hued red or pink flowers and young fruits. (An exception is S. kraemeri Harms, which has fruits green when unripe and white flowers.) However, the only important "attribute state" (cf. Jardine & Sibson, 1971, pp. 3, 4) characterizing the Brassaia group and not appearing elsewhere in Schefflera is the presence of four large, winglike, imbricated basal floral bracts. (In other Schefflera species such bracts are absent or only one to three in number and are virtually always otherwise shaped.) In addition, some species have an exceptionally large number of carpels (ovary-locules), reaching 25 to 30 in S. thaumasiantha Harms of southeastern New Guinea. However, in habit, gross morphology, overall inflorescence structure,

²Recently I have learned that the inflorescences in at least some of the capituliferous species in New Guinea act as "perches" for some birds of paradise feeding on the flowers or fruit (but not necessarily as display trees). Paradisaea raggiana (the Raggiana Bird of Paradise) has been seen on Schefflera thaumasiantha Harms in the Sogeri Plateau (C. Nicholson, pers. comm.), while Astrapia stephaniae (the Princess Stephanie Bird of Paradise) has been seen on S. lasiosphaera near Mt. Giluwe (J. Croft, pers. comm.). On a 1973 issue of Papua New Guinea postage stamps depicting birds of paradise, the 21-cent stamp illustrates the Ribbontail Bird of Paradise, Astrapia mayeri, perching on a yet-to-be-described species of Schefflera found in the Mt. Giluwe area. All these birds of paradise are at least sometimes frugivorous (Gilliard, 1969).

flowers, and fruits, the Brassaia group is very similar to the rest of the pantropical "central nexus" of Schefflera (as exemplified by such species as S. sciadophyllum (Swartz) Harms of Jamaica, S. tomentosa (Bl.) Harms of West Malesia, S. venulosa (Wight & Arnott) Harms of South India, and S. volkensii Harms of East Africa). I do not consider differences such as the presence of four large floral bracts (in contrast to three or fewer smaller bracts in other Schefflera species) and a relatively large carpel number (8 to 30) to be sufficient grounds for separation at the generic level, particularly when the strong overall resemblances with other groups of Schefflera, both in the field and on closer examina-

tion in the herbarium, are considered.

The Brassaia group seems best regarded as a section of Schefflera in a wider sense, although it is perhaps somewhat isolated. The series of species within Schefflera most closely related to the Brassaia group is that centering on S. wallichiana (Wight & Arnott) Harms, S. capitata, and S. khasiana, all of which are in mainland Asia; other sections of Schefflera within Papuasia are not as closely related to the Brassaia group. Together with the unusual features of the high average carpel number (considered a "primitive" feature by Eyde and Tseng (1971)) and the presence of the large floral bracteoles (which I believe also to be a "primitive" feature), the geographical isolation of the Brassaia group from its nearest relatives suggests that it is relictual in the Papuasian context. The very close, partly reticulate relationships of the known species also suggest that the group is presently undergoing a secondary evolutionary cycle.

In the second part of this paper I have given an annotated list of published taxa which are correctly referable to the Brassaia group. This excludes the great majority of the Brassaia combinations proposed by Hutchinson (1967). Some other Brassaia combinations of longer standing must also be excluded from the group, i.e. B. capitata (Wight & Arnott) C. B. Cl. (= Schefflera capitata (Wight & Arnott) Harms); B. sessilis (Miq.) Seem. (= S. sessilis (Miq.) Harms); and B. littorea Seem. (= S. littorea (Seem.) comb. nov.).³ As I propose to regard the group as circumscribed here at the sectional level, the correct formal name appears to be Schefflera sect. BRASSAIA (Endl.) Tseng & Hoo. When Hoo and Tseng (1965) recognized sect. BRASSAIA (Endl.) Tseng & Hoo, they included two subsections, subsect. CEPHALOSCHEFFLERA (Harms) Tseng & Hoo and subsect. ACTINOPHYLLAE (Endl.) Tseng & Hoo, the former being lectotypified by S. cephalotes (C. B. Cl.) Harms. This was the first lectotypification of the name Cephaloschefflera; Harms did not designate a type for his section CEPHALOSCHEFFLERA, and when Merrill (1923) raised section CEPHALO-SCHEFFLERA to generic rank, he did not transfer any species which Harms had originally included in that section. Although Viguier (1909) indicated that the flowers of S. cephalotes were shortly pedicellate, they ³ Basionym: Brassaia littorea Seem. Jour. Bot. London 2: 244. 1864 (Papaja litorea Rumph. Herb. Amb. 1: 151. t. 52. 1741). The species has an involved synonymy, which will be dealt with elsewhere.

are clearly aggregated into capitula, agreeing with the original description of the section, and hence S. cephalotes is a not unreasonable lectotype for section CEPHALOSCHEFFLERA. Although Hoo and Tseng (1965) should have used the sectional name CEPHALOSCHEFFLERA for a section including both S. cephalotes and S. actinophylla (Article 63 of the International Code, Stafleu et al., 1972), BRASSAIA (Endl.) Tseng & Hoo is now the correct name to use for a section which includes S. actinophylla, but not S. cephalotes. The name Brassaia has been widely used in various contexts for S. actinophylla and its allies, and it is fortunate that it can continue to be used for these plants. What of the name Cephaloschefflera? As presently typified, it appears that it will become synonymous with Blume's Aralia sect. PARA-TROPIA (1826), based partly on the umbelluliferous A. rigida Bl. (= Schefflera rigida (Bl.) Harms, presently included in S. lucescens (Bl.) Viguier), to which S. cephalotes is closely related, along with S. havilandii, S. latifoliolata, and S. hullettii. This question will be considered more fully elsewhere. The necessary break-up of the Cephaloschefflera complex has led to preliminary research toward a revision of the whole of Schefflera, together with the several segregates and closely related taxa listed elsewhere in this paper. A detailed discussion of this work is outside the scope of the present contribution. However, it is my opinion that most of the attributes used to distinguish these taxa appear to be as trivial as those indicated as distinguishing the Brassaia group from the main nexus of Schefflera, particularly when the whole assemblage of some 450 described and undescribed species is viewed. The worth of some of these attributes has already been discussed (Baumann, 1946; Philipson, 1970; Eyde & Tseng, 1971). I believe, therefore, that the best course is to reduce all of these segregates to Schefflera, except for Enochoria (which will be discussed in the third part of this paper). In subsequent papers, further details will be given concerning the 17 sections (in six subgenera) which are presently being considered for recognition. Of these sections, five (all in one subgenus) incorporate nearly all of the species formerly in the Cephaloschefflera complex, together with a large number of umbelluliferous species.

PRELIMINARY SYNOPSIS OF SCHEFFLERA SECT. BRASSAIA (AS EMENDED)

Schefflera sect. Brassaia (Endl.) Tseng & Hoo, Acta Phytotax. Sinica,

Addit. 1: 133. 1965, quoad subsect. Actinophyllae; Grushvitzky & Skvortsova, Adansonia (n. s.) 9: 386. 1969. BASIONYM: Brassaia Endl. Nov. Stirp. Dec. 89. 1839; Bentham, Fl. Austral. 3: 385. 1866; Bailey, Queensl. Fl. 2: 735. 1900; Hutchinson, Gen. Fl. Pl. 2: 73. 1967, sensu lato; Smith & Stone, Jour. Arnold Arb. 49: 489. 1968. TYPE SPECIES: S. actinophylla (Endl.) Harms (B. actinophylla Endl.).

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Schefflera sect. Cephaloschefflera Harms in Engler & Prantl, Nat. Pflanzenfam. III. 8: 36. 1894, p.p. quoad spp. actinophylla et macrostachya; Bot. Jahrb. 56: 385. 1920; Philipson, Bull. Brit. Mus. Nat. Hist. Bot. 1: 14, 15. 1951; Hutchinson, Gen. Fl. Pl. 2: 73. 1967, ut syn. Brassaiae.

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DISTRIBUTION. Aru Islands; New Guinea (mainland) and Geelvink Bay Islands (except Biak); Bismarck Archipelago (except the Admiralty Islands); Solomon Islands (including Rennell); Torres Strait Islands; northern and northeastern Australia. Also in the Caroline Islands (Truk group).

ENUMERATION OF SPECIES

Studies to date have shown that some of the species assigned to the section must or are likely to be relegated to synonymy. As far as is practicable, these reductions are indicated below. In addition, one or two additional species have yet to be described, but consideration of these is deferred until a later paper.

1. Schefflera actinophylla (Endl.) Harms in Engler & Prantl, Nat. PLATE IV-A. Pflanzenfam. III. 8: 36. 1894.

Brassaia actinophylla Endl. Nov. Stirp. Dec. 89. 1839. Brassaia singaporensis Ridley, Jour. Asiatic Soc. Straits Settlements 75: 38. 1917.

DISTRIBUTION. Australia: northeastern Queensland and northern Northern Territory; Aru Islands; New Guinea: southern and southeastern parts south of the central cordillera; Torres Strait Islands. Now escaped and naturalized in several other parts of the tropics (and subtropics).

Widely cultivated as an ornamental and street tree or as a pot plant, both indoors and out. The species is not native to the Hawaiian Islands, although otherwise indicated by Hutchinson (1967, p. 73). Brassaia singaporensis was based on escaped plants occurring on Singapore Island.

2. Schefflera brassaiella Ridley, Trans. Linn. Soc. II. Bot. 9: 65. 1916.

Schefflera pullei Harms, Bot. Jahrb. 56: 388. 1920. Brassaia brassaiella (Ridley) Hutchinson, Gen. Fl. Pl. 2: 622. 1967. Brassaia pullei (Harms) Hutchinson, Ibid. 623.

DISTRIBUTION. New Guinea: Carstensz Range east to the Hindenburg Range near Telefolmin.

The stamens of Schefflera brassaiella usually exceed the ovary-locules in number.

Schefflera corallinocarpa Harms, Bot. Jahrb. 56: 388. 1920. 3. Brassaia corallinocarpa (Harms) Hutchinson, Gen. Fl. Pl. 2: 622. 1967.

DISTRIBUTION. New Guinea: lowlands of the middle Sepik valley, near the junction of the Sepik and May rivers.

The type (Ledermann 7211) was destroyed at Berlin and no isotypes have yet been located. However, from the description it appears that the plant may be only a form of S. macrostachya.

 Schefflera kraemeri Harms, Notizbl. Königl. Bot. Gart. Berlin 5: 73. 1908; Kanehira, Jour. Coll. Agric. Kyushu Imp. Univ. 4(6): 434. 1935.

Schefflera pachyclada Kanehira, Bot. Mag. Tokyo 46: 670. 1932; Fl. Micrones. 294, fig. 148. 1933.

DISTRIBUTION. Caroline Islands: Truk group.

Distinctive in the section for its white flowers and green (in unripe stage) fruits; otherwise closely related to *Schefflera waterhousei* of the Bismarck Archipelago and the Solomon Islands. *S. pachyclada* was reduced by its author a few years after being described.

 Schefflera macrostachya (Bentham) Harms in Engler & Prantl, Nat. Pflanzenfam. III. 8: 36. 1894.

Sciadophyllum macrostachyum Bentham, London Jour. Bot. 2: 222. 1843. (As "Sciodaphyllum.")
Paratropia macrostachya (Bentham) Miq. Fl. Ind. Bat. 1(1): 760. 1856.
Brassaia macrostachya (Bentham) Seem. Jour. Bot. 2: 244. 1864; Hutchinson, Gen. Fl. Pl. 2: 623. 1967.

DISTRIBUTION. New Guinea: Japen Island in Geelvink Bay and the mainland lowlands north of the central cordillera from the Meervlakte east to the Markham-Ramu Valley near Dumpu, including the foothills of the Adalbert, Prince Alexander, Torricelli, and Van Rees ranges (so far as known). A variant form with sutures extending only part way from the apex of the corolla occurs in the Vogelkop, where it apparently replaces the more easterly form.

Schefflera macrostachya is closely related to S. actinophylla, and the two species may be considered as a vicariant pair with mutually exclusive ranges largely separated by the central cordillera. The inflorescences of the two are very similar in gross structure, but on the other hand there are some more or less constant differences in leaflet shape and venation.

The status of the Vogelkop variants remains to be determined.

6. Schefflera megalantha Harms, Bot. Jahrb. 56: 386. 1920. Brassaia megalantha (Harms) Hutchinson, Gen. Fl. Pl. 2: 623. 1967.
DISTRIBUTION. New Guinea: in the central cordillera from the Baliem-Meervlakte divide east to the Krätke Range, and on the Ramu-Astrolabe Bay dividing range west of the Finisterre Range.

The flower buds of Schefflera megalantha are distinctly cone-shaped. The species is occasionally cultivated locally (Mt. Hagen).

7. Schefflera ovalis J. J. Sm. ex Dakkus, Bull. Jard. Bot. Buitenzorg III. Suppl. 1: 262. 1930, nomen nudum.

DISTRIBUTION. Aru Islands; New Guinea: southwestern coast along the Arafura Sea from the Lorentz River to the Uta River below the Carstensz Range. Cultivated in Hortus Bogoriensis.

The name Schefflera ovalis first appears in print in Dakkus's alphabetical list of plants cultivated in Hortus Bogoriensis. It also appears on a few herbarium specimens distributed from Bogor. No description has ever been published. The plants concerned represent a form of S. actinophylla differing in its leaflets, which are coarsely toothed at the apex, and in its flower buds, which are more elongated. In addition, the leaflet venation is suggestive of S. macrostachya. The distribution of this form, as far as it is known, is just west of that of S. actinophylla in New Guinea.

8. Schefflera pachystyla Harms, Bot. Jahrb. 72: 205. 1942. PLATE IV-B.

Schefflera gigantea Philipson, Bull. Brit. Mus. Nat. Hist. Bot. 1: 14. 1951.

DISTRIBUTION. New Guinea: central cordillera from just east of Wau through the Bulolo-Watut basin to the Krätke Range, as well as in the mountains of the Huon Peninsula and the Saruwaged Range.

Both Schefflera pachystyla and S. gigantea were based on the same collection (Clemens 5386). The species is intermediate between S. megalantha and S. thaumasiantha.

 Schefflera pseudobrassaia Harms, Bot. Jahrb. 56: 388. 1920. Brassaia pseudobrassaia (Harms) Hutchinson, Gen. Fl. Pl. 2: 623. 1967. DISTRIBUTION. New Guinea: foothills of the central cordillera in the upper April River watershed, southwest of Ambunti (middle Sepik region).

The type (Ledermann 9977) was destroyed at Berlin and no isotypes have yet been located. However, the difference between the numbers of stamens and ovary-locules as described is also found in Schefflera brassaiella, as are the relatively small leaflets and short inflorescencebranches. Harms himself noted that this taxon was very close to his S. pullei, here united with S. brassaiella. It is probable that the differences given are insufficient to maintain S. pseudobrassaia as a species distinct from S. brassaiella.

 Schefflera secunda Philipson, Bull. Brit. Mus. Nat. Hist. Bot. 1: 14. 1951.

DISTRIBUTION. New Guinea: mountains of the Vogelkop.

The inflorescences of this very distinct species consist of a few spreading branches which bear numerous very small, few-flowered heads on long peduncles, all oriented upward. Another striking character is that the fruit at maturity may be as much as two-thirds superior (cf. Eyde & Tseng, 1969).

11. Schefflera stenopetala Harms, Bot. Jahrb. 56: 390. 1920. Brassaia stenopetala (Harms) Hutchinson, Gen. Fl. Pl. 2: 623. 1967.

DISTRIBUTION. New Guinea: lowlands of the middle Sepik valley near Ambunti.

The type (Ledermann 8146) was destroyed at Berlin and no isotypes have yet been located. However, the differences indicated by Harms appear to fall within the range of variation of Schefflera macrostachya; in addition, a recent collection from the Ambunti region agrees well with the description of this latter species. Consequently, it is unlikely that S. stenopetala can be maintained as distinct.

12. Schefflera thaumasiantha Harms, Bot. Jahrb. 69: 278. 1938. PLATE V-A.

DISTRIBUTION. New Guinea: in the foothill and lower montane zones of the Wharton and Owen Stanley Ranges from Tapini (north of Port Moresby) through the Sogeri Plateau to Nowata (northwest of Amazon Bay).

This spectacular species is characterized by its fruits, which have 25 to 30 or more locules, and by its inflorescence-branches, which are up to a meter or more long. It is sometimes cultivated locally (Sogeri, Brown River, Port Moresby).

13. Schefflera waterhousei Harms, Notizbl. Bot. Gart. Berlin 15: PLATE V-B. 678. 1942.

DISTRIBUTION. Bismarck Archipelago: Mussau (St. Matthias) I., New Ireland, New Britain; Solomon Islands: Bougainville to Guadalcanal and Rennell.

Schefflera waterhousei is fairly closely related to S. actinophylla, but the smaller leaflets and few-flowered heads are distinctive. The species is rather variable, although most collections fall into one of two distinct groups, of which the ranges are almost mutually exclusive. The "typical" form occurs in the northern Solomon Islands and the Bismarck Archipelago, while the other form is limited to the southern Solomon Islands. The differences may be sufficient to warrant separation at the species level, but further study is required.

A RECONSIDERATION OF THE STATUS OF ENOCHORIA

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Enochoria Baker f., a rather enigmatic araliaceous genus with one species, E. sylvicola Baker f. (1921), was originally described from one collection (Compton 1336) gathered from near Canala on the north coast of New Caledonia in 1914 and preserved in the British Museum of Natural History. This holotype collection consists of single fragments respectively of a leaf and an inflorescence. No isotypes have come to light, and to the best of my knowledge no further collections have been made. The genus was accepted without comment by Guillaumin (1948) for his Flore analytique et synoptique, as well as by Hutchinson (1967). Because of the presence of digitately compound leaves and capituliferous inflorescences, the genus was placed near Schefflera in Hutchinson's system of the family Araliaceae. In connection with the studies of the group of genera associated with Schefflera, I have re-examined the type specimen of E. sylvicola. The only conclusion that can be drawn is that the specimen is an artifact. The leaf fragment is from a species of Schefflera, probably S. affinis Baillon, while the inflorescence fragment, with flowers all carpellate, represents Meryta macrocarpa Baillon. Although both parts of the specimen carry tags with the same number, it is possible that it was not actually collected by Compton himself, but brought into camp by field workers or local residents. If the identifications of the two elements are correct, they both belong to taxa described well before 1921 and for which generic segregation is not warranted. It is therefore not possible to retain either

name for any part of the specimen. The genus Enochoria, and its sole species E. sylvicola, should therefore be rejected under Article 70 of the International Code (Stafleu et al., 1972).

SUMMARY

The long accepted division of the araliaceous genus Schefflera J. R. & G. Forst. sensu lato (including Brassaia Endl.) into two pantropical sections, CEPHALOSCHEFFLERA Harms (with flowers sessile, in capitula) and EUSCHEFFLERA (with flowers pedicellate) has been shown to be untenable. The species of the Cephaloschefflera complex represent an evolutionary grade (probably resulting from parallel retardation of pedicel growth) derived from various groups of umbelluliferous species throughout the geographical range of the complex. Special attention has been given to the status of Brassaia sensu stricto, since it has continued to be segregated from Schefflera by a number of authors, and the conclusion is reached that only sectional rank within the latter genus is warranted. Finally, an argument has been made for the reduction to Schefflera of a number of other segregate and allied genera on the grounds that the differences between most of the "attribute states" which have been used to distinguish these taxa are essentially as trivial as those used in the past to separate Brassaia. One of the segregates, Enochoria, has been shown

to have been based on an artifact. The question of the use of the name *Cephaloschefflera* for some infrageneric taxon of more restricted extent within *Schefflera* has also been discussed, with the conclusion that it could not be applied to the *Brassaia* group as presently lectotypified and is likely to become united with Blume's *Aralia* sect. PARATROPIA. An enumeration of species properly referable to sect. BRASSAIA (Endl.) Tseng & Hoo is given in the second part of this paper.

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EXPLANATION OF PLATES *

PLATE I

A (left). Diagram of inflorescence, Schefflera hoi (Dunn) Viguier (Burma, southwestern China). B (right). Diagram of inflorescence, S. capuroniana (Bernardi) Bernardi (Madagascar).

PLATE II

A (left). Diagram of inflorescence, Schefflera barteri (Seem.) Harms (West tropical Africa). B (right). Diagram of inflorescence, S. japurensis (Mart. & Zucc. ex E. March.) Harms (northern South America).

PLATE III

A (above). Inflorescence of Schefflera sp., near Kaibola, Kiriwina I., Trobriand group, New Guinea, \pm 40 m. (1972). B (below). Inflorescence of S. versteegii Harms, along upper Musgrave River, east of Sogeri Plateau, New Guinea, 200–300 m. (1971).

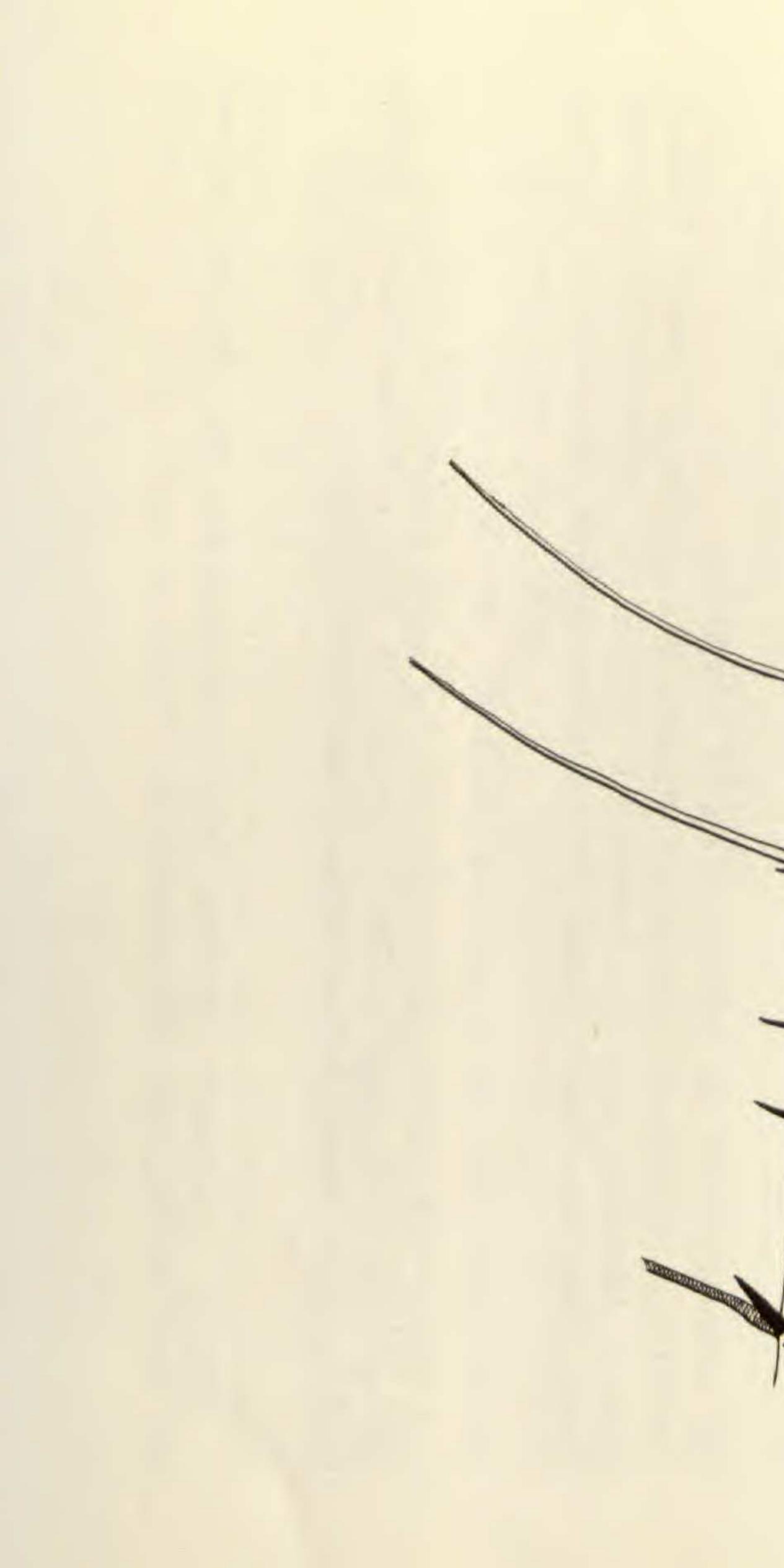
PLATE IV

A (left). Schefflera actinophylla (Endl.) Harms, Royal Botanic Gardens, Sydney, Australia, \pm 10 m. (1967). B (right). S. pachystyla Harms, near Zenag, along Lae-Bulolo Road, New Guinea, \pm 1300 m. (1972).

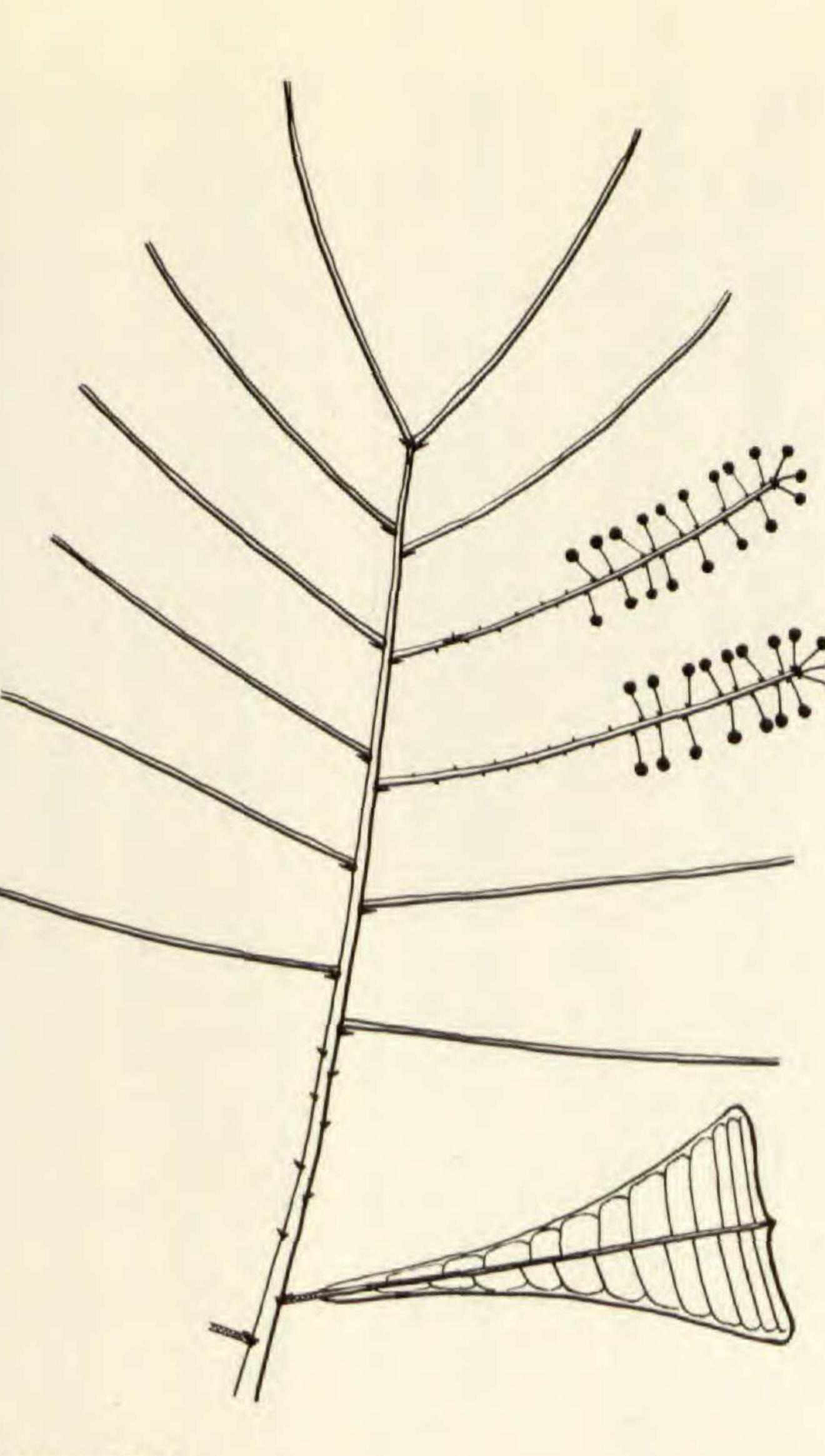
PLATE V

A (left). Schefflera thaumasiantha Harms, Sogeri Plateau, New Guinea, 500-600 m. (1974; courtesy of Mr. J. Dodd). B (right). S. waterhousei Harms, track to Lelet Plateau, New Ireland, 500-600 m. (1973).

* In the inflorescence diagrams, the cross-hatched axes near the base represent leaf bases together with their stipules (in black).

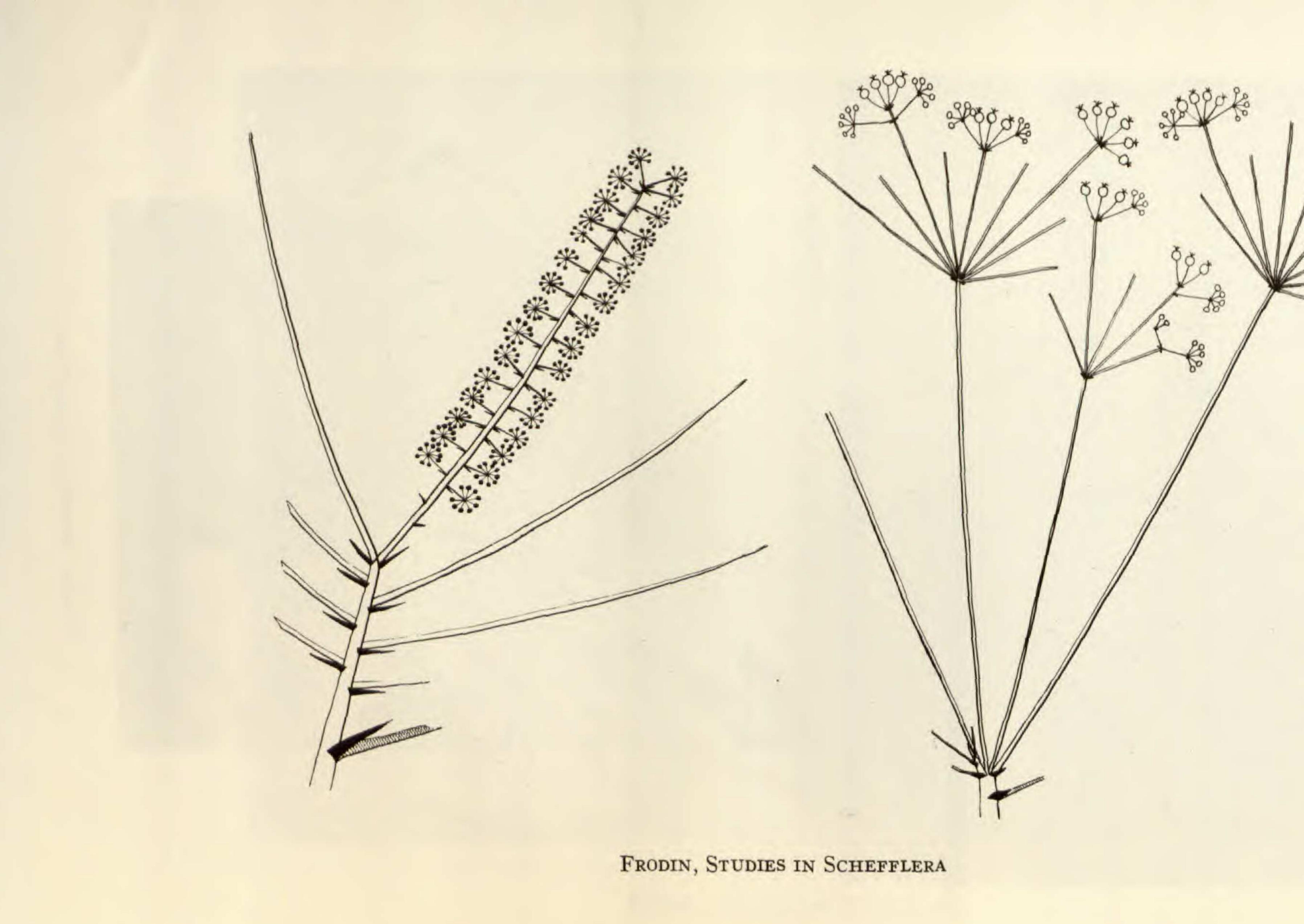


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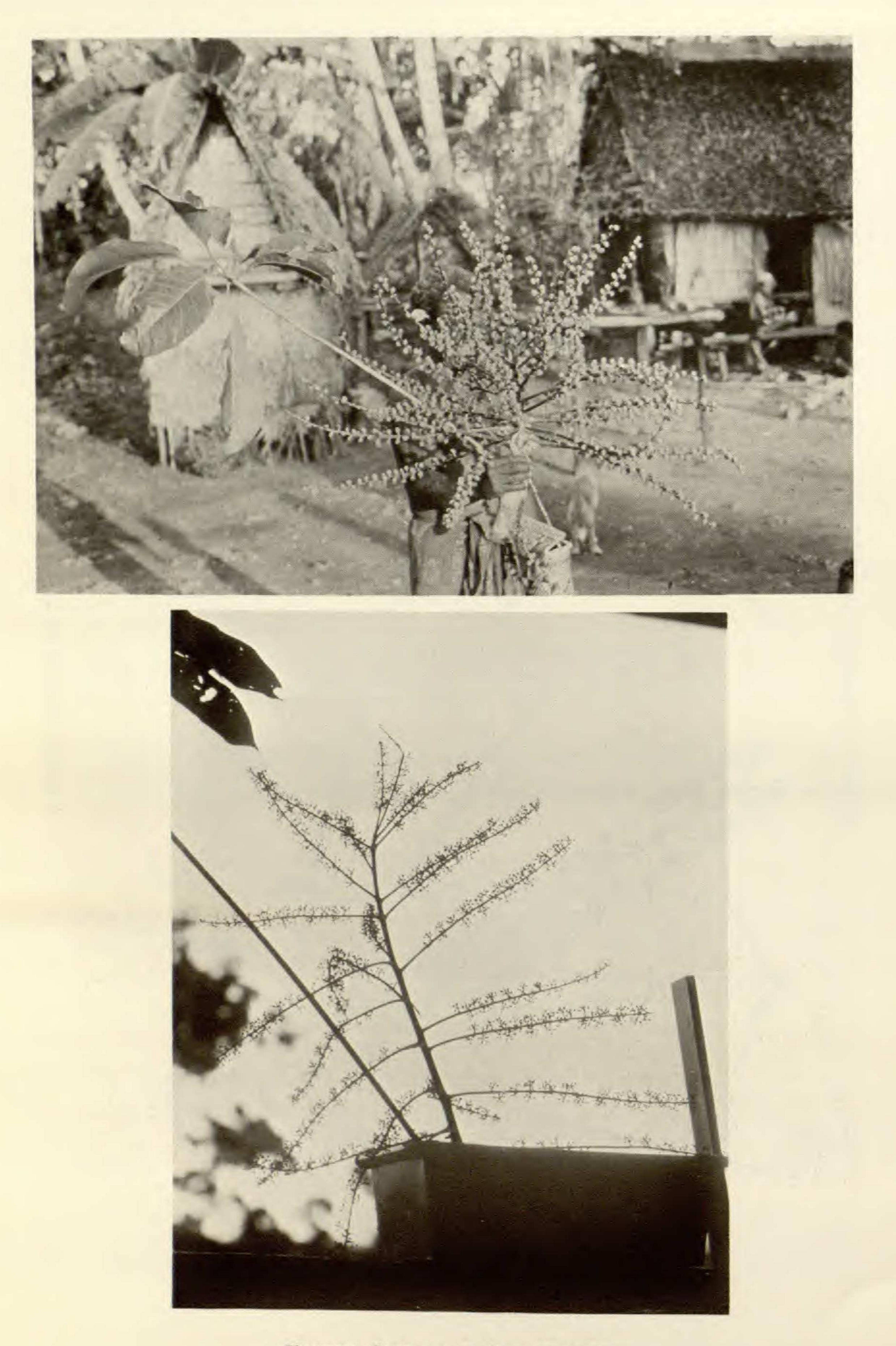
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PLATE III



FRODIN, STUDIES IN SCHEFFLERA

